

Sokatra, a New Side-Necked Turtle (Late Cretaceous, Madagascar) and the Diversification of the Main Groups of Pelomedusoides

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ABSTRACT

Sokatra antitra, n. gen. et sp., is a new side-necked turtle from the Maastrichtian (Upper Cretaceous) Maevarano Formation, Mahajanga Basin, northwestern Madagascar. *Sokatra antitra* is based on a series of incomplete skulls: a partial skull that lacks the premaxillae and some of the basicranium, a partial skull that has a complete ear region and partial basicranium, and other isolated specimens, including dentaries. Although this species exhibits some features of the North African and Brazilian Euraxemydidae, it does not belong to this family, but instead it is the sister taxon of the magnafamily Podocnemidera of Gaffney et al. (2006, 2011). Characters of *Sokatra* uniting it with the magnafamily Podocnemidera are: quadrate-basisphenoid contact, ventral covering of processus interfenestralis of opisthotic, and at least half of prootic covered ventrally. The laterally open foramen jugulare posterius and the distinct accessory ridge on the maxilla are characteristic, but not unique, features shared with members of the Euraxemydidae. The presence of a small wall posterior to the columellae auris and medial to the incisura columellae auris and the formation of the foramen posterius canalis carotici interni by both the prootic and quadrate are unique to *Sokatra*. In a PAUP analysis using the character matrix from Gaffney et al. (2006), *Sokatra* resolves as: (Pelomedusidae, *Araripemys* (*Sokatra* (Euraxemydidae (Bothremydidae, Podocnemididae)))). The deep phylogenetic roots of *Sokatra* indicates the presence of its lineage on Madagascar prior to the beginning of the Late Cretaceous.

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INTRODUCTION

Turtles split into two main groups, cryptodires and pleurodires, before the Late Triassic (Gaffney, 1990; Gaffney et al., 2006; Gaffney and Jenkins, 2010). Species of both groups survived to populate the Recent fauna, but pleurodires have been and are less diverse than cryptodires and are more restricted geographically, living at present only in the southern hemisphere. However, during the past few years, the fossil record of pleurodires has revealed a very different story, of great diversification within the Pelomedusoides (Gaffney et al., 2006; 2011). The recently discovered morphological diversity of pleurodiran skulls demonstrates a level of ecological diversity previously unknown (Gaffney et al., 2006, 2011).

Madagascar provides interesting pieces to the puzzle of pleurodiran evolution. Its extant pleurodiran fauna contains *Erymnochelys madagascariensis* (Grandidier, 1867). *Erymnochelys* is one of the more unusual endemics because all the other living members of the family are South American. There is agreement that *Erymnochelys* belongs to the Podocnemididae, but a number of conflicting phylogenetic hypotheses relate it to other members of the family, depending on whether molecular or morphologic characters are employed (Gaffney, 1988; Gaffney and Meylan, 1988; Noonan, 2000; Noonan and Chippendale, 2006; Romano and Azevedo, 2006; Vargas-Ramírez et al., 2008; Gaffney et al., 2011). Three species of the family Pelomedusidae are also found on Madagascar: *Pelomedusa subrufa* (Bonnaterre, 1789; Lacépède, 1788, made unavailable; Iverson, 1992), *Pelusios castanoides* Hewitt (1931), and *Pelusios subniger* (Bonnaterre, 1789) (Iverson, 1992, for distribution maps and synonymies; Raxworthy, 2003).

The fossil record of pleurodires from Madagascar (Lapparent de Broin, 2000; Gaffney and Forster, 2003; Gaffney et al., 2009) is essentially restricted to the Late Cretaceous (but see Samonds et al., 2009, for report of unidentified Eocene turtles). It includes a close relative of *Erymnochelys madagascariensis* but also shows the presence of at least two species of the extinct family Bothremydidae (Gaffney and Forster, 2003; Gaffney et al., 2009). In this paper we add to the diversity of Late Cretaceous pleurodirans from Madagascar by describing a new member of the Pelomedusoides, *Sokratra antitra*. This new genus and species is a basal member of the magnafamily Podocnemidera of Gaffney et al. (2006), which consists of the families Euraxemydidae, Bothremydidae, and Podocnemididae. Although *Sokratra* exhibits some features of the family Euraxemydidae, it does not belong to this family but is instead the sister taxon to its remaining members: (Pelomedusidae, *Araripemys* (*Sokratra* (Euraxemydidae (Bothremydidae, Podocnemididae)))).

For the reader's convenience, the following is a condensed summary of the classification of pleurodires from Gaffney et al. (2006, 2011) showing the higher taxon names used in this paper. The classification is abbreviated in that not all taxa included in Gaffney et al. (2006) are shown. For those interested in Madagascar, however, we include the three other known turtle taxa previously identified from the Late Cretaceous of Madagascar; they are all podocnemidids or bothremydids (Gaffney and Forster, 2003; Gaffney et al., 2009). *Sokratra* is not placed in a new higher taxon in this classification; it is indicated as the sister group to the remaining Podocnemidera by indentation.

Infraorder Cryptodira

Infraorder Pleurodira

Hyperfamily Cheloides

Hyperfamily Pelomedusoides

Magnafamily Pelomedusera

Family Pelomedusidae

Family Araripemydidae

Magnafamily Podocnemidera

Sokatra antitra n. gen. et sp.

Superfamily Euraxemydoidea

Family Euraxemydidae

Superfamily Podocnemidoidea

Family Podocnemididae

cf. *Erymnochelys*

Family Bothremydidae

Bothremydidae gen. et sp. indet.

Tribe Kurmademydini

Kinkonychelys rogersi

The reader is referred to Gaffney (1979) for the cranial morphology of turtles, with an introduction to pleurodiran cranial morphology, emphasizing the Pelomedusidae, in Gaffney et al. (2006). Further work on podocnemidids is presented in Gaffney et al. (2011). The anatomical terminology used here is available in an illustrated glossary (Gaffney, 1972; also in Gaffney, 1979). Also of relevance are the descriptions of the euraxemydids *Euraxemys* and *Dirqadim*, as well as the figures and comparative information on the pelomedusids *Pelusios* and *Pelomedusa*, all in Gaffney et al. (2006). The order and topics in the morphologic description are the same as in Gaffney et al. (2006: appendix 1) and a number of other recent papers by Gaffney and coauthors.

INSTITUTIONAL ABBREVIATIONS

FMNH The Field Museum, Chicago

UA Université d'Antananarivo, Antananarivo, Madagascar

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

INFRAORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868

MAGNAFAMILY PODOCNEMIDERA COPE, 1868

Sokatra, new genus

TYPE AND ONLY INCLUDED SPECIES: *Sokatra antitra*, n. gen. et sp.

DISTRIBUTION: Late Cretaceous (Maastrichtian) of Madagascar.

ETYMOLOGY: *Sokratra* (pronounced SOO-kah-trah), Malagasy for “turtle.”

DIAGNOSIS: Member of the magnafamily Podocnemidera by possessing prootic partially covered by basisphenoid, and processus paroccipitalis of opisthotic completely covered ventrally. Distinguished from all other Pelomedusoides by short wall of bone posterior to columellae auris, medial to incisura columellae auris; foramen posterius canalis carotici interni formed by quadrate and prootic. Distinguished from all other Podocnemidera (except Kurmademydini) by extensive temporal emargination preventing squamosal-quadratojugal and parietal-quadratojugal contacts, and exposing quadrate in temporal margin; prootic-quadratojugal contact. Distinguished from pelomedusids and *Araripemys* by deep accessory ridge on maxilla paralleling labial ridge. Additionally characterized by incisura columellae auris enclosing columellae auris and eustachian tube closed by bone, as in pelomedusids and podocnemidids; laterally open foramen jugulare posterius, as in euraxemydids; exoccipital-quadratojugal contact present, as in euraxemydids; and basisphenoid-quadratojugal contact present, as in pelomedusids, bothremydids, and podocnemidids. Lower jaw parallel sided, without any widening of the triturating surface; differs from *Euraxemys*, *Araripemys*, and pelomedusids in having a high lingual ridge forming a distinct medial margin to the triturating surface, rather than having a bladelike cross section as in *Euraxemys*, *Araripemys*, and pelomedusids. Triturating surface formed by a lingual ridge higher than labial ridge with an intervening groove or pocket.

Sokratra antitra, new species

TYPE SPECIMEN: UA 9769 (field number MAD 07433), a partial skull, lacking the premaxillae, basioccipital, and with damaged basisphenoid, quadrates, prootics, and opisthotics. The holotype skull of *Sokratra antitra* was discovered in the austral winter of 2007 as part of the joint Stony Brook University/Université d'Antananarivo Mahajanga Basin Project, which was initiated in 1993. This discovery enabled the identification and referral of most of the other, previously discovered specimens described in this report.

TYPE LOCALITY: MAD 93-35, Berivotra Study Area, northwestern Madagascar.

HORIZON: Anembalemba and Masorobe members, Maevaranano Formation, Maastrichtian, Upper Cretaceous. All of the specimens described in this report were recovered from localities in the Anembalemba and Masorobe Members (Maastrichtian, Upper Cretaceous) of the Maevaranano Formation in the Berivotra and Masiakakoho study areas, Mahajanga Basin, northwestern Madagascar (see description and map in Gaffney et al., 2009: fig. 1). Geographic coordinates for these localities are on file at the Field Museum (Chicago), Stony Brook University, and the Université d'Antananarivo and are available to qualified investigators.

DIAGNOSIS: As for genus.

ETYMOLOGY: *Antitra* (pronounced AHN-tah-trah), Malagasy for “old.”

REFERRED SPECIMENS: FMNH PR 2649 (field number MAD 07673), a partial skull with articulated or associated quadrates (both right and left), opisthotics (both right and left), left exoccipital, right prootic, left pterygoid, and right palatine; UA 9864 (field number MAD 07637), a partial right quadrate; and UA 9865 (field number MAD 07862), a partial left maxilla.

These three specimens are referred to *Sokratra antitra* based on direct comparisons and morphological agreement with the holotype. Five other incomplete specimens are more tentatively referred: FMNH PR 2647 (field number MAD 07581), supraoccipital; FMNH PR 2648 (field number MAD 07583), left frontal; UA 9770 (field number 96144), right parietal; UA 9771 (field number MAD 05564), right dentary; UA 9866 (field number MAD 07895), left dentary.

In addition to the holotype specimen, FMNH nos. PR 2647–PR 2649 and UA nos. 9864 and 9865 were recovered from a small (2 m²) quarried surface in locality MAD 93-35 (Berivotra Study Area). UA 9770 was collected from locality MAD 93-34 (Berivotra Study Area) and UA 9771 was collected from locality MAD 05-61 (Masiakakoho Study Area). UA 9866 was collected from locality MAD 07-66 (Berivotra Study Area), which lies stratigraphically in the Masorobe Member of the Maevarano Formation; it is the only specimen not recovered from the Anembalemba Member.

Shell material was not found associated with any of the *Sokratra* skull elements, but the relatively common presence of pleurodire shell material in these units suggests that at some time it may be possible to associate shell morphology with *Sokratra*.

DESCRIPTION

PREFRONTAL (figs. 1, 2, 5)

PRESERVATION: Both prefrontals are present in UA 9769.

CONTACTS: The prefrontal in *Sokratra* meets the prefrontal on the midline, the maxilla anteroventrolaterally, and the frontal posteriorly, as in other Pelomedusoides. The frontal sends a process anteriorly on the ventral surface along the midline, preventing the prefrontal from roofing the sulcus olfactorius.

STRUCTURES: The dorsal plate of the prefrontal forms the dorsal margin of apertura narium externa, which is slightly protruding on the midline, similar to the condition in *Podocnemis*. The prefrontal also forms the anterodorsal margin of the orbit. On the ventral surface, the prefrontal forms the roof of the fossa nasalis, which is a shallow concavity just lateral to the midline. As in pelomedusids and euraxemydids, the prefrontal in *Sokratra* has a ventral process projecting anteroventrolaterally that forms the edge of the foramen orbito-nasale.

FRONTAL (figs. 1, 2, 5)

PRESERVATION: Both frontals are present in UA 9769 but they do not have clear posterior sutures. An isolated left frontal, FMNH PR 2648, is well preserved and, although incomplete, helps with the identification of the frontal sutures and the ventral morphology. This disarticulated frontal is a pleurodire as indicated by the presence of a sulcus palatinoptyergoideus; it is also possible that it belongs to the bothremydids *Kinkonychelys* (Gaffney et al., 2009), but we consider this unlikely because *Kinkonychelys* has a deeper ridge for the sulcus palatinoptyergoideus compared to *Sokratra*. Nonetheless, it might belong to a taxon not yet identified from the Maevarano Formation. Neither the diagnosis nor any of the phylogenetic characters rely

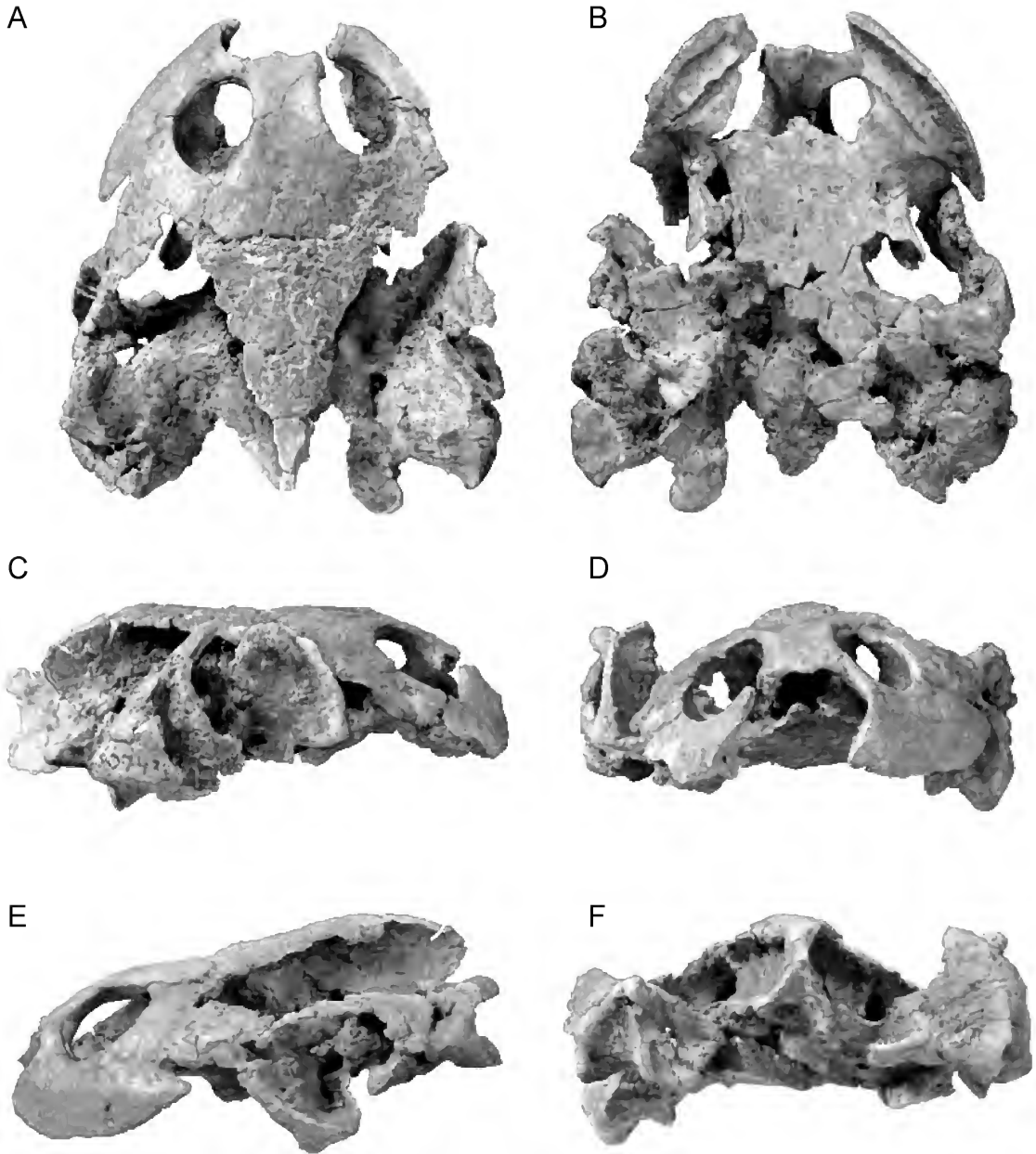


FIG. 1. *Sokatra antitra*, n. gen. et sp. UA 9769, holotype skull. A, dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior.

on FMNH PR 2648 belonging to *Sokatra*.

CONTACTS: The frontal in UA 9769 (best preserved on the right side) contacts the frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, and the parietal posteriorly. The latter contact is poorly preserved and not clearly visible in UA 9769; it is also not visible in

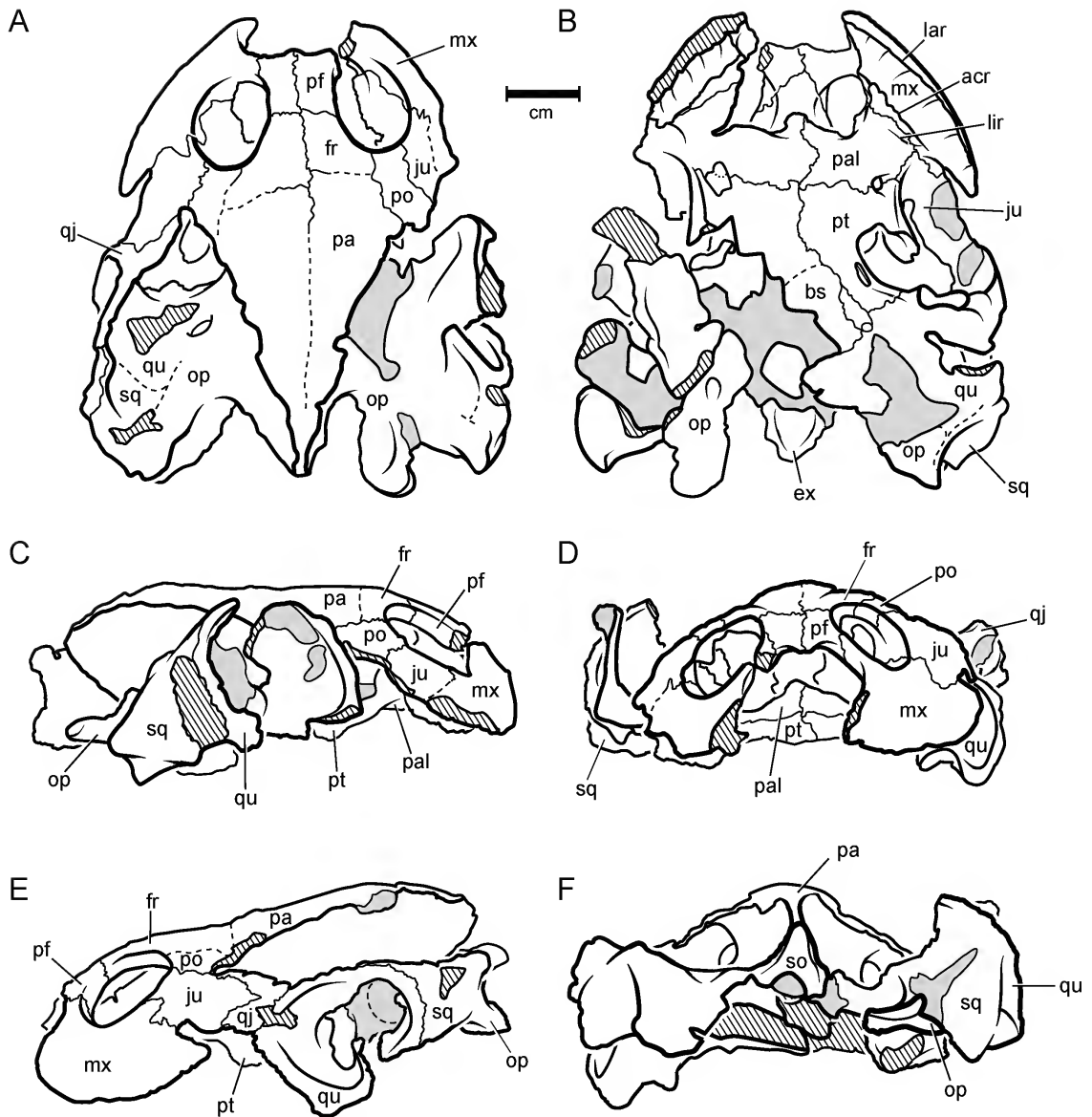


FIG. 2. *Sokratra antitra*, n. gen. et sp. Key to figure 1. UA 9769, holotype skull. A, dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior. Abbreviations: **acr**, accessory ridge; **bs**, basisphenoid; **ex**, exoccipital; **fr**, frontal; **ju**, jugal; **lar**, labial ridge; **lir**, lingual ridge; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **po**, postorbital; **pt**, pterygoid; **qj**, quadratojugal; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal.

FMNH PR 2648, in which the posterior edge is broken. Nonetheless, considering these specimens and the isolated parietal, UA 9770, it can be deduced that the frontal has a posterolateral contact with the postorbital similar to that in pelomedusids except that it is relatively short. Similarly, as restored, the postorbital contact with the frontal is longer in *Sokratra* than in pelomedusids.

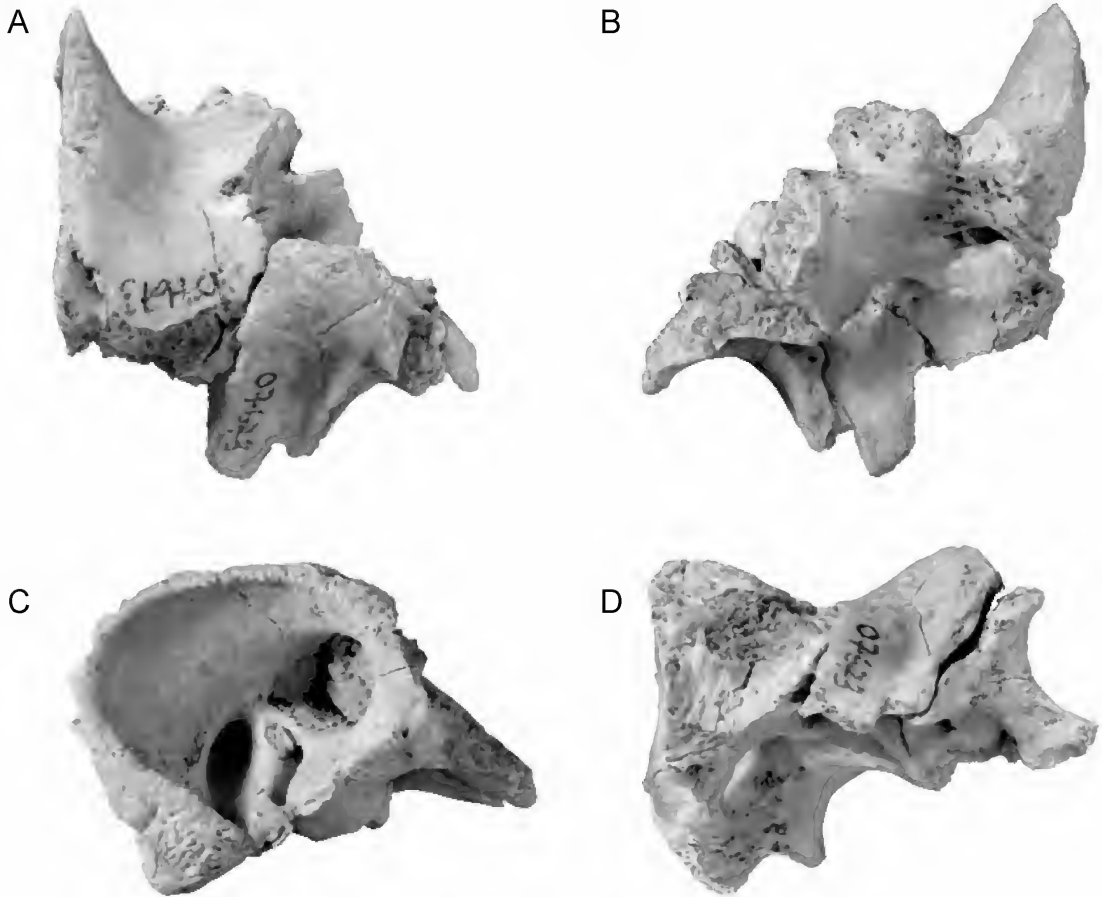


FIG. 3. *Sokatra antitra*, n. gen. et sp. FMNH PR 2649, posterolateral portion of skull. **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, posterior.

STRUCTURES: The frontal forms the posteromedial portion of the orbital margin. *Sokatra* has a temporal emargination comparable to that seen in pelomedusids and *Araripemys*, in contrast to the more completely roofed skulls of euraxemydids, bothremydids, and podocnemidids. On the ventral surface, the frontal forms most of the sulcus olfactorius. Lateral to the sulcus it forms a low ridge paralleling the orbital margin that separates the orbit from the sulcus palatinoptyergoideus. The frontal forms the anterior part of the sulcus palatinoptyergoideus, as in other pleurodires (Gaffney et al., 2006: fig. 25).

PARIETAL (figs. 1, 2, 5)

PRESERVATION: Both parietals are present but poorly preserved in UA 9769, with the sutures distinguishable only with difficulty. A disarticulated parietal, UA 9770, is identified as *Sokatra* on the basis of the extremely close agreement with the parietal in UA 9769.

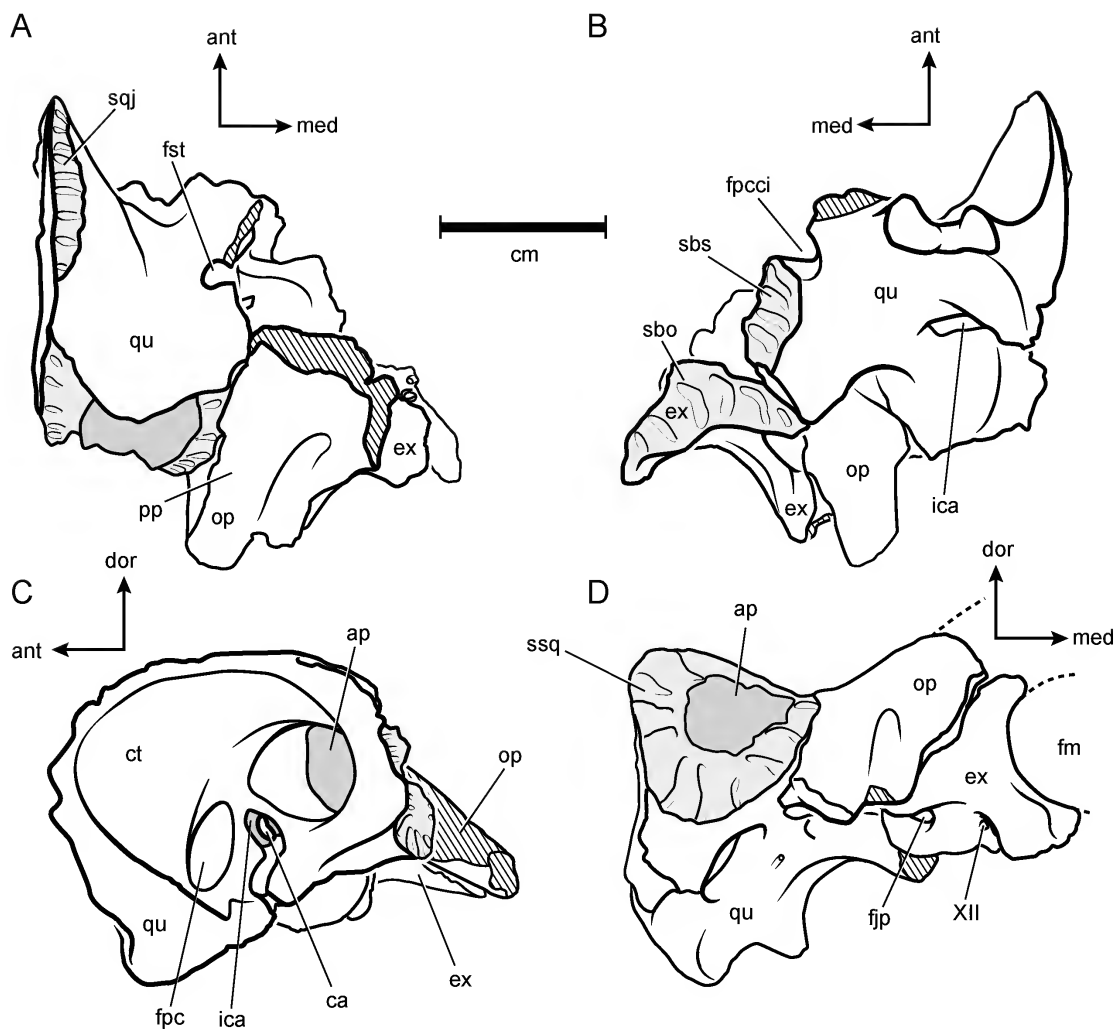


FIG. 4. *Sokatra antitra*, n. gen. et sp. Key to figure 3. FMNH PR 2649, posterolateral portion of skull consisting of the left quadrate, opisthotic, and exoccipital. Dark grey is matrix, light grey is sutural surface, hatched is broken bone edge. **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, posterior. Abbreviations: **ant**, anterior; **ap**, antrum postoticum; **ca**, columella auris; **ct**, cavum tympani; **dor**, dorsal; **ex**, exoccipital; **fjp**, foramen jugulare posterius; **fm**, foramen magnum; **fpc**, fossa precolumellaris; **fpcci**, foramen posterius canalis carotici interni; **fst**, foramen stapedio-temporale; **ica**, incisura columellae auris; **med**, medial; **op**, opisthotic; **pp**, processus paroccipitalis; **qu**, quadrate; **sbo**, sutural surface with basioccipital; **sbs**, sutural surface with basisphenoid; **sqj**, sutural surface with quadratojugal; **ssq**, sutural surface with squamosal; **XII**, foramen nervi hypoglossi.

CONTACTS OF DORSAL PLATE: As in pelomedusids, euraxemydids, and other Pelomedusoides, the contacts of the parietal in *Sokatra* are with the parietal on the midline, the frontal anteriorly, and the postorbital anterolaterally. The postorbital contact is not well preserved in any specimen but, based on both UA 9769 and UA 9770, it is relatively narrow, due to the extent of the temporal emargination in *Sokatra*.

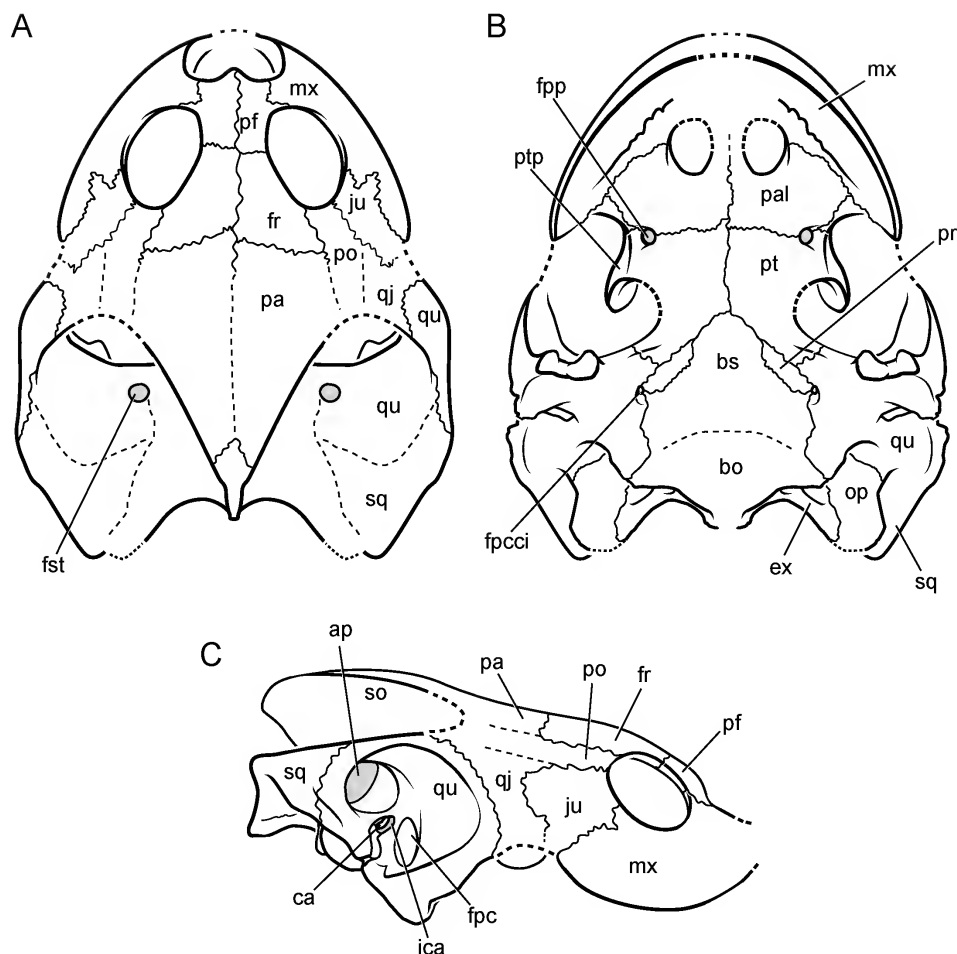


FIG. 5. *Sokatra antitra*, n. gen. et sp. Reconstruction of skull based on UA 9769, holotype skull, and FMNH PR 2649, referred partial skull. **A**, dorsal; **B**, ventral; **C**, lateral. Abbreviations: **ap**, antrum postoticum; **bo**, basioccipital; **bs**, basisphenoid; **ca**, columella auris; **ex**, exoccipital; **fpc**, fossa precolumellaris; **fpcci**, foramen posterius canalis carotici interni; **fpp**, foramen palatinum posterius; **fr**, frontal; **fst**, foramen stapedio-temporale; **ica**, incisura columella auris; **ju**, jugal; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **po**, postorbital; **pr**, prootic; **pt**, pterygoid; **ptp**, processus trochlearis pterygoidei; **qj**, quadratojugal; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal.

Pelomedusids, unlike euraxemydids, have no parietal-quadratojugal contact. Although this area is poorly preserved in UA 9769, and the referral of UA 9770 is not certain, UA 9769 is well enough preserved to show that a parietal-quadratojugal contact is very unlikely.

STRUCTURES OF DORSAL PLATE: The temporal emargination in *Sokatra* extends anteriorly to expose the foramen stapedio-temporalis and all the otic chamber in dorsal view, a condition typical of pelomedusids and *Araripemys*, but not found in Podocnemidera (including Euraxemydidae). UA 9769 has a temporal emargination that is narrower posteriorly than in *Kinkonychelys* and podocnemidids. On the ventral surface, the parietal forms the posterior part of

the shallow sulcus palatinopterygoideus.

CONTACTS OF PROCESSUS INFERIOR PARIETALIS: The processus inferior parietalis is very poorly preserved in UA 9769, and lacking a ventral edge in UA 9770. Although the ventral contacts are not determinable, those of the pterygoid, prootic, and supraoccipital are so universal in turtles that their presence is highly likely. Based on the anterior extent of the processus inferior parietalis in UA 9769, it is also very likely that a palatine-parietal contact was present, as in pelomedusids, euraxemydids, and many other Pelomedusoides. On the ventral surface of the right parietal in UA 9769, it can be seen that there is no parietal-ptyerygoid contact above the processus trochlearis pterygoidei.

STRUCTURES OF PROCESSUS INFERIOR PARIETALIS: As preserved in UA 9769, the processus inferior parietalis of *Sokatra* is similar to that in pelomedusids, euraxemydids, and most other Pelomedusoides, as this structure does not vary much in this group. The foramen nervi trigemini is identifiable on the left side of UA 9769 and seems to be formed by the usual elements: the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

JUGAL (figs. 1, 2, 5)

PRESERVATION: The lateral plate of the jugal is present on both sides of UA 9769; the sutures are relatively clear except that the maxilla is broken on both sides to a varying extent so the exact position of the cheek emargination is not definite. The medial process is not as well preserved, but most of its sutures can be seen on the left side.

CONTACTS OF LATERAL PLATE: The jugal contacts the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posterodorsally, as in pelomedusids. The posterior contact with the quadratojugal is V-shaped with the apex pointing posteriorly. As this unusually shaped contact is preserved only on one side of one damaged specimen, it might be considered suspect, but the shape of this suture can be seen on the internal surface as well.

STRUCTURES OF LATERAL PLATE: The jugal of *Sokatra* is of about the same relative size as in pelomedusids and euraxemydids, but not as large as in *Podocnemis*. The jugal forms the posteroventral part of the orbital rim. It probably contributes to the anterior part of the cheek emargination, although this is not preserved in any specimen. On the left side of UA 9769 there is only a small part of the jugal missing, and it is likely that this part entered the cheek emargination rather than the quadratojugal sending a process ventrally to meet the maxilla. As seems likely based on this area of UA 9769, the cheek emargination in *Sokatra* was not as extensive dorsally as in *Podocnemis*, but very similar to that in pelomedusids and euraxemydids.

CONTACTS OF MEDIAL PROCESS: In the floor of the orbit (in dorsal view), the jugal contacts the maxilla anteriorly and laterally. It probably contacts the palatine medially on the left side of UA 9769, but this is obscured by breakage. In the septum orbitotemporale the jugal in UA 9769 has the usual pelomedusid and euraxemydid contacts with the postorbital dorsomedially, the palatine ventromedially, the pterygoid posteriorly, and the maxilla ventrally.

STRUCTURES OF MEDIAL PROCESS: The jugal in UA 9769 forms part of the fossa orbitalis floor, as in pelomedusids and euraxemydids, and the lateral part of the septum orbitotemporale,

as in other Pelomedusoides. The jugal does not extend onto the triturating surface.

QUADRATOJUGAL (figs. 1, 2, 5)

PRESERVATION: The quadratojugal is present only in UA 9769 on the left side and it is incomplete. The dorsal margin is a broken edge, although the edge is very thin and probably did not extend much farther. The ventral margin is mostly broken but a small section of finished margin shows the extent of the cheek emargination. The posterior contact with the quadrate is broken, but the position of most of the suture is determinable.

CONTACTS: The quadratojugal in UA 9769 contacts the quadrate posteriorly, the jugal anteriorly, and, probably, the postorbital anterodorsally. The latter contact is not actually visible but is likely. There is no squamosal-quadratojugal contact in *Sokatra*, but both *Pelusios* and *Pelomedusa* have narrow ones. The absence of a quadratojugal-parietal contact, which appears to be the case in *Sokatra*, is characteristic of pelomedusids and *Araripemys*, but it is present in euraxemydids, podocnemidids, and many bothremydids.

STRUCTURES: The quadratojugal in UA 9769 is a flat plate entering the cheek emargination ventrally and the temporal emargination dorsally.

SQUAMOSAL (figs. 1, 2, 5)

PRESERVATION: The squamosal in *Sokatra* is present on both sides of UA 9769; both are largely complete but damaged with some crushed areas.

CONTACTS: The squamosal in *Sokatra* contacts the quadrate anteriorly and anteromedially, and the opisthotic medially, on the dorsal, posterior, and ventral surfaces. Due to the temporal emargination there is no contact with the quadratojugal. *Sokatra* differs from pelomedusids, euraxemydids, and *Araripemys* in having no contact between the squamosal and quadratojugal above the cavum tympani of the quadrate. In *Araripemys* and many pelomedusids the contact between these bones is very narrow, but in *Sokatra* they are widely separated, exposing a substantial length of quadrate in the temporal margin.

STRUCTURES: The squamosal in *Sokatra* has the usual conical shape, with a large antrum postoticum internally.

POSTORBITAL (figs. 1, 2, 5)

PRESERVATION: The postorbital in *Sokatra* is present on both sides of UA 9769, but both are incomplete. The left one has a broken posterior margin and the dorsal contact is in a broken area, particularly posteriorly, while the right one is more complete but also has a broken posterior margin.

CONTACTS OF LATERAL PLATE: The postorbital definitely contacts the frontal anteromedially, the jugal ventrally, and the parietal posteromedially. It probably contacts the quadratojugal posteroventrally, but this is not actually preserved.

STRUCTURES OF LATERAL PLATE: The postorbital in *Sokatra* forms part of the dorsal margin of the orbit. It probably also formed part of the temporal margin posteriorly, but this is broken on both sides. Nonetheless, a small part of the edge of the right postorbital is very thin and seems to be close to or on the temporal margin, showing that there is no quadratojugal-parietal contact and that the postorbital does form part of the temporal emargination. All of these features of the cheek are very similar in *Sokatra*, euraxemydids, and pelomedusids.

CONTACTS OF MEDIAL PROCESS: In the septum orbitotemporale, facing the fossa orbitalis, the postorbital contacts the frontal dorsomedially and the jugal ventrolaterally. Neither of these is well preserved. Facing the fossa temporalis, the postorbital contacts the parietal dorsomedially, the jugal ventrolaterally, and, probably, the pterygoid ventromedially.

STRUCTURES OF MEDIAL PROCESS: The postorbital forms most of the roof of the sulcus palatinoptyergoideus, which is relatively thin as in pelomedusids. It is thicker in euraxemydids. The ventral surface has a shallow concavity forming the roof of the sulcus palatinoptyergoideus.

PREMAXILLA

The premaxillae are not preserved in any of the available specimens of *Sokatra*.

MAXILLA (figs. 1, 2, 5)

PRESERVATION: Both maxillae are present in UA 9769 but have some breakage; the left is more complete than the right. An isolated but fragmentary left maxilla, UA 9865, is also referred.

CONTACTS OF VERTICAL PLATE: The maxilla in UA 9769 contacts the jugal posterodorsally, the prefrontal anterodorsally, and, were it present, the premaxilla anteromedially. It is possible that a short quadratojugal contact was present posteriorly, but this is unlikely.

STRUCTURES OF VERTICAL PLATE: The maxilla in *Sokatra* is similar to that in pelomedusids and euraxemydids, forming the ventral margin of the orbit, the lateral margin of the apertura narium externa, and the anterior margin of the cheek emargination. The extent of cheek emargination in *Sokatra* is similar to that in pelomedusids and euraxemydids.

The ventral rim of the orbit is not at the same level as the floor of the fossa orbitalis, and there is a more distinct rim separating them. *Pelusios* tends not to have this low rim, but *Pelomedusa* has one that approaches the condition in *Sokatra*.

CONTACTS OF HORIZONTAL PLATE: As preserved, the maxilla in UA 9769 contacts the palatine posteromedially and the jugal posterolaterally. It is likely that there had been a premaxilla contact anteriorly. The palatine contact extends onto the triturating surface slightly, much as in pelomedusids and podocnemidids. The jugal does not extend onto the triturating surface.

STRUCTURES OF HORIZONTAL PLATE: The triturating surface in *Sokatra* is slightly wider than in pelomedusids, much wider than in *Araripemys*, but similar to that in euraxemydids. As the anterior limits of the maxillae are not preserved and the edges of the apertura narium

Table 1. Measurements of *Sokratra antitra* UA 9769 (see Gaffney et al., 2006: fig. 315, for positions of skull measurements; D1 is left orbital width, D2 is right orbital width, J1 is height of left orbit, J2 is height of right orbit). All measurements in mm.

	A	B	C	D1	D2	E	F	G	H	I	J1	J2	K	L	M	N	O
UA 9769	indet	62.0	9.5	14.0 ^a	13.5	13.0 ^a	18.6 ^a	28.0	indet	63.6	11.0	indet	21 ^a	indet	8.8	16.4 ^a	43.4 ^a

^a Measurement estimated from damaged area.

interna are incomplete, the exact shape of the triturating surface is not known, but it seems to be parallel sided as in pelomedusids and euraxemydids, rather than triangular, as in bothremydids. *Sokratra* has a strong, narrow labial ridge, deeper than in euraxemydids, pelomedusids, and *Araripemys*. *Sokratra* has a prominent accessory ridge formed on the maxilla, deeper and more acute than in pelomedusids and euraxemydids, but in about the same position as that seen in most *Pelusios* species. The ridge in *Sokratra* is closely parallel to the labial ridge, while in *Euraxemys* the ridge trends anterolaterally and does not precisely parallel the labial ridge. In *Dirqadim*, however, the accessory ridge is much more similar to that in *Sokratra*, as it is deep and does parallel the labial ridge. The lingual ridge in *Sokratra* forms the most medial margin of the triturating surface, parallels the labial and the accessory ridges, and is low or absent.

VOMER

The vomer is missing in all available specimens of *Sokratra*. Considering the fragile nature of this element, this does not mean that the bone was absent in life. The anterior margins of the palatines are broken and the premaxillae are missing, both areas that could help determine the presence or absence of the vomer in *Sokratra*.

PALATINE (figs. 1, 2, 5)

PRESERVATION: Both palatines are present in UA 9769 but are incomplete and with unclear sutures, particularly on the dorsal surface. However, FMNH PR 2649 has a disarticulated palatine that is nearly complete.

CONTACTS: As in pelomedusids, euraxemydids, and other Pelomedusoides, the palatine of *Sokratra* contacts the maxilla anterolaterally, the palatine medially on the midline, and the pterygoid posteriorly. There is a dorsal surface contact with the processus inferior parietalis.

STRUCTURES ON DORSAL SURFACE: The palatine forms part of the fossa orbitalis floor, the posterior edges of the apertura narium interna, and the anterior margin of the foramen palatinum posterius, which penetrates to the ventral surface.

STRUCTURES ON VENTRAL SURFACE: The palatine reaches the edge of the posteromedial part of the triturating surface and, along with the maxilla, forms the choanal passages.

QUADRATE (figs. 1–5)

PRESERVATION: Both quadrates are present but incomplete and with poorly preserved margins in UA 9769. Although not well preserved, the major features of the quadrate can be discerned in this specimen. However, in the partial skull, FMNH PR 2649, both quadrates are well preserved without crushing or distortion, and the right one is nearly complete. In this specimen the contacts and features are clear. Another specimen, UA 9864, is the lower portion of a right quadrate, but it reveals little not also seen in UA 9769 and FMNH PR 2649. The very close similarity in quadrate morphology (i.e., the relatively large and deep fossa precolumellaris, the large antrum postoticum, and the incisura columellae auris that contains the columellae auris and eustachian tube) allows the confident identification of UA 9769, UA 9864, and FMNH PR 2649 as belonging to the same taxon.

CONTACTS ON LATERAL SURFACE: The quadrate of *Sokatra* contacts the quadratojugal anterodorsomedially and the squamosal posterodorsally, as in pelomedusids, euraxemydids, and many other Pelomedusoides. The quadrates in both UA 9769 and FMNH PR 2649 preserve a finished edge along the dorsalmost margin, demonstrating that the squamosal and quadratojugal do not contact, as they do in pelomedusids, euraxemydids, and other Podocnemidera.

STRUCTURES ON LATERAL SURFACE: The cavum tympani in *Sokatra* has an incisura columellae auris that agrees in morphology with those of pelomedusids and *Araripemys* but differs from those of euraxemydids in having a relatively large opening enclosing both the columellae auris and eustachian tube. *Sokatra* has a very narrow contact, like that in *Pelusios sinuatus*, closing the incisura rather than a wider more extensive contact, as in *Pelomedusa*. In *Araripemys* and euraxemydids, the incisura is open distally. The fossa precolumellaris in *Sokatra* is relatively large, as in pelomedusids, and larger than in *Araripemys*. In euraxemydids, this fossa is shallow. The antrum postoticum in *Sokatra* is relatively large and deep, also as in pelomedusids and *Araripemys*. It is slightly smaller in euraxemydids. However, the antrum is not quite as large as in the Indian and Malagasy bothremydids *Kurmademys* and *Kinkonychelys*, respectively (Gaffney et al., 2001, 2009). Although the variation of the antrum postoticum provides characters among the pleurodires, it is also guilty of a lot of homoplasy.

CONTACTS ON DORSAL AND ANTERIOR SURFACE: These contacts are clear only in FMNH PR 2649, with some information from UA 9769. The quadrate contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly and posterolaterally, as in all Pelomedusoides.

STRUCTURES ON DORSAL AND ANTERIOR SURFACE: The foramen stapedio-temporale is poorly preserved in UA 9769 but is better preserved in FMNH PR 2649. It is formed between the quadrate and prootic, as in other turtles, and it is in the more dorsal position within that suture as in pelomedusids, euraxemydids, and podocnemidoids, in contrast to the more anterior position in bothremydids (Gaffney et al., 2006).

CONTACTS ON VENTRAL SURFACE: Unfortunately, the ventral contacts around the quadrate and pterygoid are not clear in any of the specimens. However, FMNH PR 2649 preserves a left

pterygoid and quadrate, and UA 9769 does show some sutures among the cracks. The quadrate contacts the pterygoid anteromedially, the prootic medially, the exoccipital posteriorly, and the basisphenoid medially. The exoccipital contact is not found in pelomedusids and *Araripemys*, but it is characteristic of euraxemydids, bothremydids, and podocnemidids. The contact is the result of the medial process of the quadrate in *Sokatra* extending posteriorly to underlie the processus interfenestralis of the opisthotic and reach the exoccipital, and is not in the same position as in euraxemydids. In euraxemydids the exoccipital has a ventral process that is exposed on the surface next to the basioccipital (Gaffney et al., 2006: fig. 44), but in *Sokatra* there is no ventral process of the exoccipital and that bone contacts the quadrate right on the medial quadrate process. The contact area in *Sokatra* is also larger than in euraxemydids. It should be noted that the coding of this character changes *Sokatra* from sister to Euraxemydidae, if stated as a simple presence or absence, to sister to all other Podocnemidera, if multiple states are used. The latter is closer to what appears to be reality (always a vague concept in systematics) and has been adopted here.

Strictly speaking, the quadrate-basioccipital contact is not determinable as that bone is missing in all available specimens; however, given the positions, sizes, and preserved contact areas of the quadrate, exoccipital, and basisphenoid (what is known of it), this contact is very likely and has been indicated in the restoration (fig. 5B; also see discussion under Basioccipital). The quadrate in FMNH PR 2649 has preserved a sutural surface that is very difficult to interpret as anything but a posteromedial basioccipital contact (fig. 4B), due to the absence of a ventral process of the exoccipital.

STRUCTURES ON VENTRAL SURFACE: In the quadrates of FMNH PR 2649 and UA 9769, there is a notch for the foramen posterius canalis carotici interni that is formed between the quadrate posteriorly and the prootic anteriorly. In UA 9769 the area has a number of cracks, but a likely foramen is preserved on the left side between the prootic anteriorly and the quadrate posteriorly.

The condylus mandibularis in *Sokatra* is in a very similar position to that in pelomedusids, euraxemydids, and *Araripemys*, well anterior to the condylus occipitalis and anterior to the basisphenoid-basioccipital contact (presumed position in *Sokatra*). *Sokatra* has what appears to be a very shallow fossa pterygoidea, which is absent in pelomedusids, but a shallow one is present in euraxemydids.

CONTACTS ON POSTERIOR SURFACE: The quadrate in *Sokatra* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, the basioccipital ventromedially (very likely but not definite, see Basioccipital), and the prootic ventromedially, as in pelomedusids and euraxemydids.

STRUCTURES ON POSTERIOR SURFACE: The fenestra postotica in FMNH PR 2649 shows incomplete subdivisions for the lateral head vein and stapedia artery, as in euraxemydids. The aditus canalis stapedio-temporalis leads anteriorly as in other turtles. The fenestra postotica in *Sokatra* is unique among pleurodires in having a wall of bone between it and the base of the incisura columellae auris. It does not enclose the columellae auris in a canal as in bothremydids, but it does separate the columellae auris from the eustachian tube medial to the base

of the incisura columellae auris. The incisura columellae auris of *Sokatra*, as seen in lateral view through the cavum tympani, still has the typical oval shape as seen in pelomedusids and podocnemidids, containing both the columellae auris and the eustachian tube. The incisura is open in euraxemydids and *Araripemys*. The foramen chorda tympani inferius lies on the posterior surface of the processus articularis, as in most Pelomedusoides.

PTERYGOID (figs. 1, 2, 5)

PRESERVATION: The pterygoid is present in both UA 9769 and FMNH PR 2649. In FMNH PR 2649 there is a left pterygoid lacking the processus trochlearis pterygoidei, while in UA 9769 both pterygoids are present but the right one is represented only by part of the processus trochlearis pterygoidei and associated fragments. The left one is more complete, lacking only the pterygoid flange, but the bone is not well preserved and contacts are not clear.

CONTACTS ON VENTRAL SURFACE: The pterygoid in *Sokatra* contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, the prootic posteriorly, and the quadrate posterolaterally.

STRUCTURES ON VENTRAL SURFACE: The processus trochlearis pterygoidei in *Sokatra* is well preserved only on the left side of UA 9769. The angle of the processus is acute, as in euraxemydids and pelomedusids, rather than close to a right angle, as in podocnemidids.

The pterygoid in *Sokatra* is well enough preserved to conclude that it is unlikely that the pterygoid formed any part of the foramen posterius canalis carotici interni. The foramen palatinum posterius lies in the palatine-ptyergoid suture, as in other pleurodires.

CONTACTS ON DORSAL SURFACE: UA 9769 has the dorsal pterygoid surfaces present but poorly preserved, and FMNH PR 2649 lacks the processus trochlearis pterygoidei. The preserved contacts of the processus trochlearis pterygoidei are with the jugal anterolaterally, and the palatine anteroventrally. Possible postorbital contacts are not determinable.

STRUCTURES ON DORSAL SURFACE: The pterygoid forms the floor of the sulcus palatino-ptyergoideus, as in other pleurodires. The foramen nervi vidiani, usually in the vicinity of the foramen palatinum posterius, is not visible. In the disarticulated pterygoid of FMNH PR 2649, the crista pterygoidea, foramen nervi trigemini, and sulcus and canalis cavernosus, are all visible. They are similar in morphology to those structures in pelomedusids and euraxemydids.

SUPRAOCCIPITAL (figs. 1, 2, 5)

PRESERVATION: The supraoccipital is present and complete in UA 9769. However, its contacts with surrounding elements are not clear.

CONTACTS: The only suture preserved is with the parietal on the skull roof, showing that some of the supraoccipital is exposed on the skull roof.

STRUCTURES: The crista supraoccipitalis in *Sokatra* is relatively short, as in pelomedusids and euraxemydids.

EXOCCIPITAL (figs. 1–5)

PRESERVATION: The exoccipital in *Sokatra* is present and complete on the left side of FMNH PR 2649.

CONTACTS: The exoccipital in *Sokatra* contacts the opisthotic dorsolaterally, the quadrate ventrolaterally, and, based on the sutural surfaces of the exoccipital and quadrate in FMNH PR2649, the basioccipital ventrally. A basisphenoid contact is not determinable.

STRUCTURES: The exoccipital, along with the supraoccipital, forms the foramen magnum. Although incomplete due to the absence of the basioccipital, the exoccipital sutural surface looks as if the condylus occipitalis included the basioccipital as well as the exoccipitals. There are two foramina nervi hypoglossi recessed into a depression at the base of the condylus occipitalis. The foramen jugulare posterius is only partially closed in *Sokatra*, as in euraxemydids. It is closed in pelomedusids.

BASIOCCIPITAL (fig. 5)

PRESERVATION: The basioccipital is missing in all available specimens of *Sokatra*. However, due to the presence of sutural surface areas on what are interpreted as contacting bones, some of the features of the basioccipital can be determined with a reasonable degree of certainty.

CONTACTS: FMNH PR 2649, a posterolateral portion of the skull consisting of the left quadrate, opisthotic, and exoccipital (figs. 3, 4), shows what is very likely to be the exoccipital-basioccipital and the quadrate-basioccipital contacts. It can be concluded that the exoccipital is covered by the basioccipital-quadrate contact ventrally, as indicated in figure 5B, even though the basioccipital itself is not preserved. The basioccipital contacts the exoccipital dorsally and the quadrate anterolaterally.

STRUCTURES: Although the objective determination of some sutures is possible, recognition of actual structures is beyond even my imagination.

PROOTIC (figs. 1–5)

PRESERVATION: Both prootics are present in UA 9769; the right one is poorly preserved and missing its ventral half whereas the left one is mostly complete, but its dorsal portion is poorly preserved. Sutures are not visible on the dorsal surface, but the ventral surface of the left prootic shows some sutures among the cracks. FMNH PR 2649 includes a well-preserved right prootic that is missing only some of its ventral edges. The description of the prootic in *Sokatra* is based on both specimens but FMNH PR 2649 is the most useful in revealing morphological detail.

CONTACTS: The only prootic sutures that can be confirmed are with the quadrate laterally, the supraoccipital posterodorsally, the parietal dorsomedially, the pterygoid ventrally, the basisphenoid medially, and the opisthotic posteriorly, all as in pelomedusids and euraxemydids. Although we have restored the ventral exposure of the prootic between the quadrate/pterygoid and basisphenoid, based on UA 9769 and FMNH PR 2649, the positions of these sutures are

still open to interpretation. Enough of the prootic is preserved in the various specimens to show that neither the exoccipital nor the prootic are exposed between the basioccipital and quadrate (fig. 5B).

STRUCTURES: In the fossa temporalis, the prootic in *Sokatra* forms the posteroventral margin of the foramen nervi trigemini along with the pterygoid and parietal, as in most Pelomedusoides, except bothremydids where it is close to the foramen stapedio-temporale. The foramen stapedio-temporale is formed as is usual in turtles, in the suture with the quadrate, and is visible in dorsal view.

Within the cavum acustico-jugulare, the prootic forms the margin of the fenestra ovalis, along with the opisthotic, and the foramen cavernosum, along with the quadrate, as in all other Pelomedusoides. On the medial surface of the prootic is the hiatus acusticus and the recessed fossa acustico-facialis. The foramen nervi facialis can be followed from the fossa ventrally to its opening in the canalis caroticus internus on the ventral surface. The foramen nervi acustici lies in its usual position above the foramen nervi facialis in the fossa. The cavum labyrinthicum is visible and, to the extent it is visible, is morphologically similar to that in other Pelomedusoides.

One of the key areas for characters useful in analyzing basal Pelomedusoides, is the posterolateral basicranial surface, the area of the foramen posterius canalis carotici interni and the prootic (Gaffney et al., 2006: figs. 276, 277). Unfortunately, this area is poorly preserved in *Sokatra* and some interpretations are necessary to reach conclusions about characters here. In UA 9769, there is a narrow strip of prootic exposed between the pterygoid anterolaterally, the quadrate posterolaterally, and the basisphenoid medially. The well-preserved prootic in *Sokatra*, FMNH PR 2649, shows some of the ventral exposure, but the margin of the foramen posterius canalis carotici interni itself has been broken away due to the very fragile nature of the margin. Nonetheless, the canalis caroticus internus is preserved with the ventral opening of the facial nerve in its roof, so presumably the more ventral opening of the facial nerve, the foramen nervi facialis proper, as seen in ventral view, should be nearby. Unfortunately, the other specimen of *Sokatra*, UA 9769, has cracks in this area that are as large as possible foramina. However, there is a foramen seen in both specimens at the posterior edge of the prootic, formed also by the quadrate, that seems to be the foramen posterius canalis carotici interni. The canalis caroticus internus is preserved in the prootic in FMNH PR 2649, and it extends from the basisphenoid sutural surface posterolaterally to the quadrate sutural surface, where the foramen posterius canalis carotici interni is formed.

The most important missing area in *Sokatra* is posterior to the hypothesized position of the foramen posterius canalis carotici interni. The basisphenoid is mostly missing, as is the entire basioccipital. Nonetheless, it is clear that the prootic is not exposed posteriorly between the basioccipital and quadrate (see Basioccipital and Quadrate).

Pelomedusids and *Araripemys* show the primitive condition for the foramen posterius canalis carotici interni in Pelomedusoides. In these taxa the foramen posterius canalis carotici interni is usually formed entirely in the prootic (with some thin slips of basisphenoid variably entering it), and the prootic is entirely or almost entirely exposed in ventral view. In *Euraxemys*

the prootic is partially covered ventrally, as in *Sokatra*, but in *Euraxemys* the foramen posterius canalis carotici interni is formed anteriorly between the basisphenoid and the pterygoid. In *Dirqadim*, another euraxemydid, the prootic is covered partially as well, but the foramen posterius canalis carotici interni is formed between the pterygoid and prootic. In both euraxemydids the foramen posterius canalis carotici interni lies at the anterior end of the prootic, in contrast to *Sokatra*, which has it at the posterior end of the prootic. Another significant difference is that in *Sokatra* the quadrate and basisphenoid contact posterior to the prootic and foramen posterius canalis carotici interni, but in the euraxemydids the quadrate does not extend that far posteriorly, a presumably primitive condition within the magnafamily Podocnemidera. The Bothremydidae and Podocnemididae, which make up the superfamily Podocnemidoidea within the magnafamily Podocnemidera, have a well-developed quadrate-basisphenoid contact. *Sokatra*, then, has a combination of the primitive prootic at least partially forming the foramen posterius canalis carotici interni, combined with a derived quadrate-basisphenoid contact. The position of the foramen posterius canalis carotici interni seems to be best interpreted as primitive at this level, but being placed at the posterior end of the prootic with a quadrate margin is unique and therefore difficult to homologize with other relevant taxa.

OPISTHOTIC (figs. 1–5)

PRESERVATION: Portions of both opisthotics are present in UA 9769, but they are poorly preserved. In FMNH PR 2649 both are present and well preserved.

CONTACTS: Although the basioccipital is missing, it is unlikely that a basioccipital-opisthotic contact was present in *Sokatra* because the left side of FMNH PR 2649 shows the ventral limits of the opisthotic and the exoccipital-quadrate contact would prevent an opisthotic-basioccipital contact. The opisthotic in *Sokatra* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially.

STRUCTURES: The fenestra postotica shows the slight division of the lateral head vein (more medial) from the stapedia artery (more lateral, mostly formed by the quadrate), as in many Pelomedusoides. The processus interfenestralis of the opisthotic is completely covered ventrally, in contrast to the condition in pelomedusids and *Araripemys*, and as in euraxemydids and other Podocnemidera. As in euraxemydids and pelomedusids the opisthotic forms the fenestra ovalis (with the prootic) and the fenestra perilymphatica, visible in FMNH PR 2649. The cavum labyrinthicum is also visible in this specimen and it does not vary among the relevant taxa. The cavum acustico-jugulare is roofed by the opisthotic and limited laterally by the quadrate wall behind the columellae auris (see Quadrate).

BASISPHEOID (figs. 1, 2, 5)

PRESERVATION: The basisphenoid in *Sokatra* is preserved only in a small area on the ventral surface of UA 9769 where its contacts are barely discernible and interpretable. Bone fragments

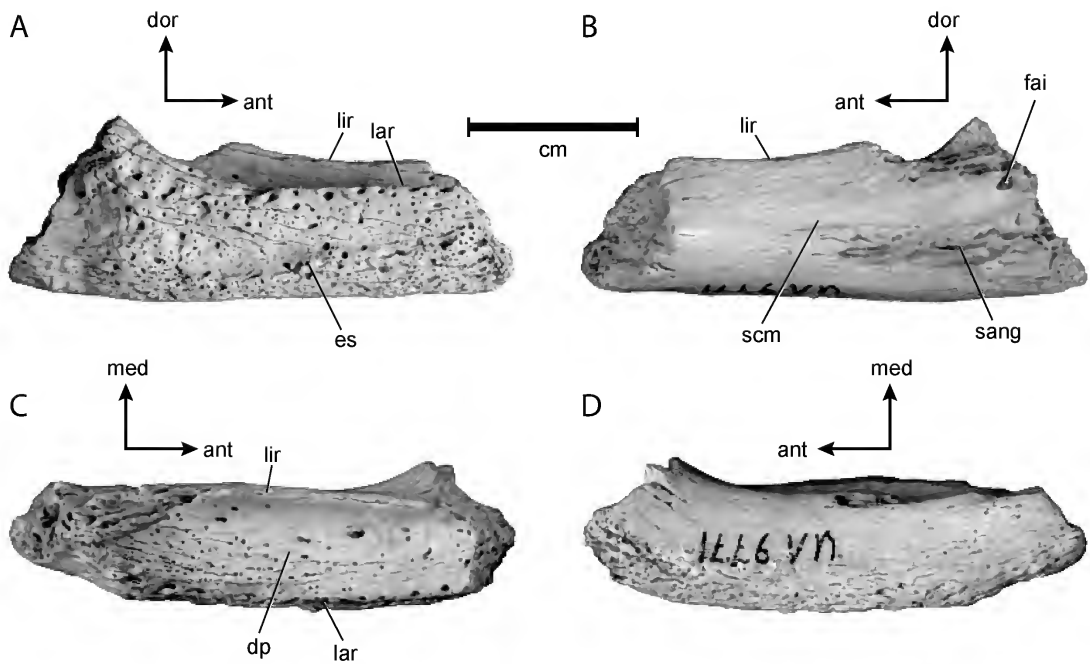


FIG. 6. *Sokatra antitra*, n. gen. et sp. UA 9771, partial right dentary. **A**, lateral; **B**, medial; **C**, dorsal; **D**, ventral. Orientations are approximate as rami are at an angle to midline in life. Abbreviations: **ant**, anterior; **dor**, dorsal; **dp**, dentary pocket; **es**, external shelf; **fai**, foramen alveolare inferius; **lar**, labial ridge; **lir**, lingual ridge; **med**, medial; **sang**, sutural surface with angular; **scm**, sulcus cartilaginis meckelii.



FIG. 7. *Sokatra antitra*, n. gen. et sp. UA 9771, dorsal view of partial lower jaw restored by reversing right dentary (using fig. 6C) and rotating around presumed midline based on skull reconstruction in figure 5. Anterior to top of page.

and matrix cover its dorsal surface. Contacting the basisphenoid posteriorly are some pieces of flat bone that do not belong to this skull. These are too thick to be parts of the basisphenoid or other missing elements. Flat bone fragments are also inside the skull, along with some extant plant roots.

CONTACTS: The basisphenoid is poorly preserved but seems to contact the pterygoid anteriorly, the prootic laterally, and the quadrate in a short suture posteriorly.

STRUCTURES: Virtually none are discernible. The basisphenoid is flat with possibly a very minute spur reaching the margin of the foramen posterius canalis carotici interni, although this is doubtful.

DENTARY (figs. 6, 7)

PRESERVATION: Two isolated, partial dentaries, UA 9771 (right ramus) and UA 9866 (left ramus), are tentatively referred to *Sokratra antitra* because of the complementary nature of their triturating surfaces compared with those of the triturating surfaces of the skull. The agreement includes the presence of a high accessory ridge on the maxilla, complemented by strong labial and lingual ridges on the dentary with an intervening trough. UA 9771 lacks most of the symphysis and all postdentary elements; UA 9866 also lacks most of the symphyseal area but has a few remnants of the angular, although these are fragments.

CONTACTS: Based on the preserved sutural contact areas present on the dentary, it has the usual Pelomedusoides contacts with both the coronoid dorsomedially and the angular postero-ventrally, represented only by sutural surfaces in UA 9771, but some bone fragments are retained in UA 9866. The angular contact extends anteriorly on the medial surface to about the degree seen in *Euraxemys* and most other Pelomedusoides. The coronoid area is incomplete but is more restricted ventrally than in *Euraxemys* (Gaffney et al., 2006: fig. 232), suggesting that *Sokratra* has a larger anterior opening to the foramen intermandibularis medius, as in Podocnemididae and Bothremydidae.

STRUCTURES: The dentary in *Sokratra* is similar in proportions to that in *Podocnemis*, wider than in *Euraxemys* but much narrower than in typical bothremydids. It is parallel sided, without a widening of the triturating surface. *Sokratra* differs from *Euraxemys*, *Araripemys*, and pelomedusids in having a high lingual ridge forming a distinct medial margin to the triturating surface, rather than having a more bladelike cross section as in these more basal Pelomedusoides.

The triturating surface in *Sokratra* is distinctive among Pelomedusoides in having a high lingual ridge, a lower labial ridge, and a concave intervening groove. This arrangement is similar to that seen outside the pleurodires, in the trionychoid genera, *Adocus* and *Baptemys* (Meylan and Gaffney, 1989: figs. 9, 10). These authors termed the groove the dentary pocket, as in these cryptodires it has a distinct anterior margin to the pocket formed by the anteromedial position of the lingual ridge which reaches the labial ridge to close off the pocket. We use the term for *Sokratra* even though it seems to lack this anterior margin (because it is not completely preserved on the symphysis the anterior limits of the dentary pocket are unknown in *Sokratra*).

The dentary pocket in *Sokratra* could extend anteriorly as the shallow groove seen in *Podocnemis* and other Pelomedusoides.

The dentary pocket (fig. 6) in *Sokratra* received the accessory ridge (fig. 2B) of the maxillary triturating surface. The accessory ridge on the maxilla in *Sokratra* is also matched by an accessory ridge in *Adocus* and *Baptemys*. The dentary pocket in *Sokratra* has a rounded cross section, also as in *Adocus* and *Baptemys*. The external surface of the dentary in *Sokratra* has a poorly defined horizontal shelf probably separating the more dorsal rhamphotheca of the beak from the ventral skin-covered bone of the rest of the jaw. This shelf is relatively lower in UA 9771 and much higher in UA 9866.

The lingual ridge in UA 9771 is a thin wall with a rounded but narrow apex. In UA 9866 the lingual ridge is wider with a flat surface developed along its length. Whether this is the result of individual variation, age, or different species is unknown.

On the internal surface of the dentary in *Sokratra* (UA 9771) the sulcus cartilaginis meckelii is not as distinct as in *Euraxemys* and the other basal Pelomedusoides, but it does not appear to have been formed into a canal. Posteriorly the foramen alveolare inferius lies in almost the same position as it does in *Euraxemys* (Gaffney et al., 2006: figs. 231, 232).

The living podocnemidids have lower jaws relatively similar to one another. They all have roughly parallel-sided triturating surfaces with a low labial ridge, a higher lingual ridge, and a shallow intervening trough. The lingual ridge is usually higher than the labial ridge and the lingual ridge frequently has some expansion or flattened surface dorsally. These jaws differ from *Sokratra* in lacking the well-developed groove we have termed the dentary pocket, as well as having lower labial ridges and a smooth external surface without the horizontal shelf seen in *Sokratra*. The lower jaw of an unknown Miocene podocnemidid described by Gaffney et al. (1998; possibly belonging to *Caninemys*) agrees with *Sokratra* in some of these features (high labial and lingual ridges, dentary pocket), but differs in having the labial ridge terminate anteriorly abruptly in a conelike dorsal projection.

CONCLUSIONS

Sokratra antitra is the fourth pleurodiran taxon to be recognized from the Late Cretaceous of Madagascar, the others being relatively derived forms (Gaffney and Forster, 2003; Gaffney et al., 2009). The relationships of *Sokratra* have been hypothesized using the character matrix from Gaffney et al. (2006); taxa with high amounts of missing data were removed, as in that paper. The results are shown in figure 8. The analysis was done using all the taxa shown in the most parsimonious cladogram 1 of Gaffney et al. (2006, fig. 288) but, in the cladogram shown here as figure 8, all of the bothremydid genera have been placed in their tribes for graphic convenience. Four trees of 414 steps resulted from our analysis of 47 taxa and 175 characters (one character parsimony uninformative). All characters were unweighted, the consistency index is 0.58, and the retention index is 0.80. *Sokratra* resolves as the sister taxon to Euraxemydidae plus Podocnemidoidea (= Podocnemididae + Bothremydidae). It could also be expressed as (Pelomedusidae, *Araripemys* (*Sokratra* (Euraxemydidae (Bothremydidae, Podocnemididae)))).

Table 2. Comparison of *Sokatra* and other Pelomedusoides

	Pelomedusidae	<i>Araripemys</i>	<i>Sokatra</i>	Euraxemydidae	Bothremydidae	Podocnemididae
Temporal emargination	extensive	extensive	extensive	slight to moderate	slight (except in Kurmademydini)	slight
Parietal-quadratojugal contact	absent	absent	absent	present	present (absent in Kurmademydini)	present
Quadratojugal-squamosal contact	present	present	absent	present	present (absent in Kurmademydini)	present
Accessory tritürating ridge	absent to small	absent	large	present but small	present and absent	present and absent
Columellae auris and eustachian tube separated by bone	no	no	no	no	yes	no
Incisura columellae auris enclosing columellae auris and eustachian tube by bone	yes	no	yes	no	no	yes
Partial wall behind columellae auris	absent	absent	present	absent	absent, stapedial canal in different position	absent
Foramen posterius canalis carotici interni	prootic and basisphenoid	prootic	quadrate and prootic	pterygoid, basisphenoid and prootic	variable but not in prootic	variable but not in prootic
Pterygoid forms at least part of foramen posterius canalis carotici interni	no	no	no	yes	yes	yes
Fossa precolumellaris	deep	deep	deep	shallow	absent (except in Kurmademydini)	present, usually deep
Quadrate-basioccipital contact	absent	absent	?	absent	present	present
Foramen jugulare posterius	closed	variable	open	open	closed and open	closed
Exoccipital-quadrate contact	absent	absent	present	present	present	absent
Prootic covered ventrally	no	no	in part	in part	yes	yes
Processus interfenestralis covered ventrally	no	no	yes	yes	yes	yes
Opisthotic projects posteriorly beyond squamosal	yes	yes	yes	yes	no	yes
Basisphenoid-quadrate contact	narrow	absent	narrow	absent	narrow and wide	wide
Prootic-quadrate contact	present	present	present	present	absent	absent
Condylus occipitalis	exoccipital	exoccipital and basioccipital	exoccipital and basioccipital	exoccipital and basioccipital	exoccipital alone, exoccipital and basioccipital	exoccipital and basioccipital

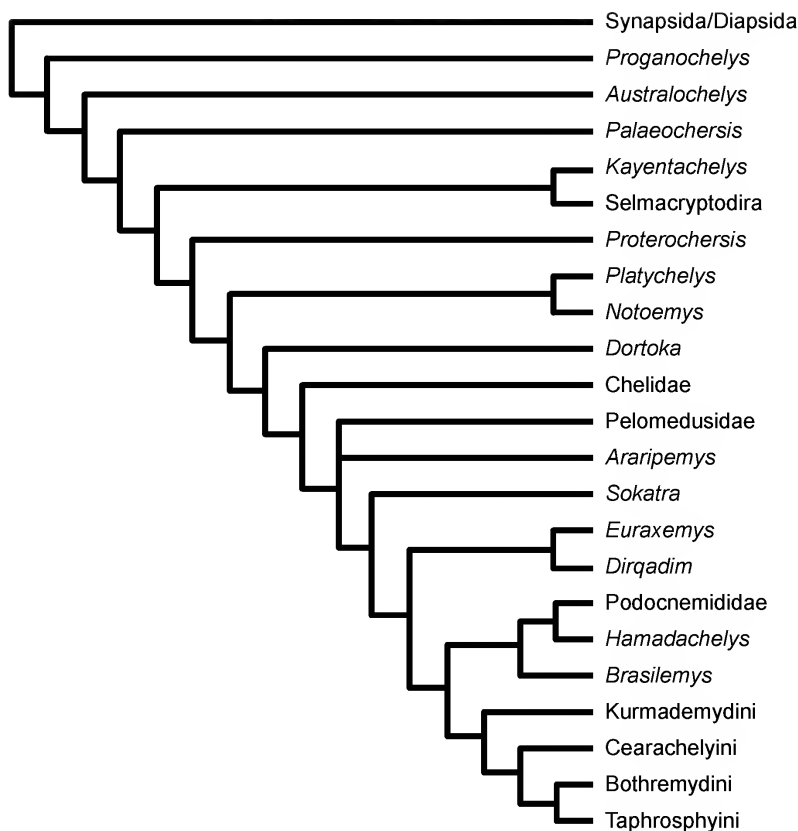


FIG. 8. Consensus cladogram of four equally parsimonious cladograms from a PAUP analysis resulting in 414 steps, using 47 taxa and 175 characters (one character parsimony uninformative), all characters unweighted, with a consistency index of 0.58 and a retention index of 0.80. Taxa and character matrix from Gaffney et al. (2006) (genera in the family Bothremydidae have been reduced to their tribes for graphic convenience, see Gaffney et al., 2006: fig. 288, for the full complement of bothremyd taxa).

Sokatra was basically a “living fossil” in the Late Cretaceous. It was a sister taxon to the two main groups of Pelomedusoides, the Bothremydidae and Podocnemididae, both of which had extensively diversified by the time of the *Sokatra* fossils available to us. The biogeographic significance of this is unclear and gives further credence to the idea that the biogeography of turtles was long and complex.

Sokatra has a number of primitive characters for Pelomedusoides (e.g., extensive temporal emargination, deep fossa precolumellaris and antrum postoticum, and foramen posterius canalis carotici interni formed at least in part by prootic). Characters of *Sokatra* uniting it with the magnafamily Podocnemidera are: quadrate-basisphenoid contact, ventral covering of processus interfenestralis of opisthotic, and at least half of prootic covered ventrally. The laterally open foramen jugulare posterius and the distinct accessory ridge on the maxilla are characteristic, but not unique, features shared with members of the Euraxemydidae. The presence of a small wall posterior to the columellae auris and medial to the incisura columellae auris and the formation of the foramen

posterius canalis carotici interni by both the prootic and quadrate are unique to *Sokratra*. There are no significant character contradictions with *Sokratra* as a basal member of the magnafamily Podocnemidera of Gaffney et al. (2006, 2011), and it is clearly resolved within the group. Features distinguishing *Sokratra* from other Pelomedusoides taxa are summarized in table 2.

As the large sister group to *Sokratra* includes taxa with ages of at least Albian (Gaffney et al., 2006), it is likely that *Sokratra* represents a biogeographic signal in Madagascar that significantly predates the Maastrichtian (latest Late Cretaceous) fauna in which it is preserved. Of relevance in this regard are several genera from the Albian of Brazil (e.g., *Euraxemys*, *Brasilemys*, *Cearachelys*) and the Cenomanian of Morocco (e.g., *Dirqadim*, *Hamadachelys*, *Galianemys*) that presumably represent a broad Gondwanan distribution of pleurodires prior to the final opening of the Atlantic Ocean and separation of South America from Africa near the Early/Late Cretaceous boundary. Furthermore, the biogeographic pattern suggested by our phylogeny places *Sokratra* in a group that has distributional patterns older than the bothremydids, which are also known from the Maastrichtian of Madagascar (Gaffney and Forster, 2003; Gaffney et al., 2009) and the Indian subcontinent (Gaffney et al., 2001, 2003). Madagascar was, prior to the Coniacian, still sutured to the Indian subcontinent and together they formed the Indo-Madagascar landmass, along with the Seychelles (Storey et al., 1995, 1997; Torsvik et al., 2000). Assuming a restricted capacity for dispersal across marine barriers, the presence of *Sokratra* and Kurmademydini (Bothremydidae) in the latest Cretaceous of Madagascar may represent the legacy of ancient lineages that persisted after isolation of Indo-Madagascar from other Gondwanan landmasses in the Early Cretaceous (Ali and Aitchison, 2009; Ali and Krause, 2011).

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REFERENCES

- Ali, J.R., and J.C. Aitchison. 2009. Kerguelen Plateau and the Late Cretaceous southern-continent bio-connection hypothesis: tales from a topographical ocean. *Journal of Biogeography* 36: 1778–1784.

- Ali, J.R., and D.W. Krause. 2011. Late Cretaceous bio-connections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography* 38: 1855–1872.
- Bonnaterre, A. 1789. *Erpétologie. In Tableau encyclopédique et méthodique des trois règnes de la nature.* Paris: Chez Panckoucke. 28+70 pp.
- Cope, E.D. 1864. On the limits and relations of the Raniformes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 16: 181–183.
- Cope, E.D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20: 242–300.
- Gaffney, E.S. 1972. An illustrated glossary of turtle skull nomenclature. *American Museum Novitates* 2486: 1–33.
- Gaffney, E.S. 1979. Comparative cranial morphology of Recent and fossil turtles. *Bulletin of the American Museum of Natural History* 164 (2): 1–376.
- Gaffney, E.S. 1988. A cladogram of the pleurodiran turtles. *Acta Zoologica Cracoviensia* 31 (15): 487–492.
- Gaffney, E.S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History* 194: 1–263.
- Gaffney, E.S., and C.A. Forster. 2003. Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar. *American Museum Novitates* 3397: 1–13.
- Gaffney, E.S., and F.A. Jenkins. 2010. The cranial morphology of *Kayentachelys*, an Early Jurassic cryptodire, and the early history of turtles. *Acta Zoologica* 91 (3): 335–368.
- Gaffney, E.S., and P.A. Meylan. 1988. A phylogeny of turtles. *In* M.J. Benton (editor), *The phylogeny and classification of the tetrapods. Vol. 1, Amphibians, reptiles, birds.* Systematics Association Special Volume 35A: 157–219.
- Gaffney, E.S., K.E. Campbell, and R.C. Wood. 1998. Pelomedusoid side-necked turtles from Late Miocene sediments in southwestern Amazonia. *American Museum Novitates* 3245: 1–12.
- Gaffney, E.S., S. Chatterjee, and D.K. Rudra. 2001. *Kurmademys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India. *American Museum Novitates* 3321: 1–16.
- Gaffney, E.S., D.W. Krause, and I.S. Zalmout. 2009. *Kinkonychelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar. *American Museum Novitates* 3662: 1–25.
- Gaffney, E.S., P.A. Meylan, R.C. Wood, E. Simons, and D.A. Campos. 2011. Evolution of the side-necked turtles: the Family Podocnemididae. *Bulletin of the American Museum of Natural History* 350: 1–237.
- Gaffney, E.S., A. Sahni, H. Schleich, S.D. Singh, and R. Srivastava. 2003. *Sankuchemys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India. *American Museum Novitates* 3405: 1–10.
- Gaffney, E.S., H. Tong, and P.A. Meylan. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History* 300: 1–698.
- Grandidier, A. 1867. Liste des reptiles nouveaux découverts, en 1866, sur la côte sud-ouest de Madagascar. *Revue Magazine Zoologique de Paris* 19 (2): 232–234.
- Hewitt, J. 1931. Descriptions of some African tortoises. *Annals of the Natal Museum* 6: 461–506.
- Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Richmond, IN:

privately printed, 363 pp.

- Lacépède, B.G.E. 1788. *Histoire naturelle des quadrupèdes ovipaires et des serpens*. Vol. 1. Paris: Imprimerie du Roi, 668 pp.
- Lapparent de Broin, F. de. 2000. African chelonians from the Jurassic to the present: phases of development and preliminary catalogue of the fossil record. *Palaeontologia Africana* 36: 43–82.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th ed., tomus 1. Holmiae [Stockholm]: Laurentii Salvii, 824 pp.
- Meylan, P.A., and E.S. Gaffney. 1989. The skeletal morphology of the Cretaceous cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea. *American Museum Novitates* 2941: 1–60.
- Noonan, B. 2000. Does the phylogeny of pelomedusoid turtles reflect vicariance due to continental drift? *Journal of Biogeography* 27: 1245–1249.
- Noonan, B.P., and P.T. Chippindale. 2006. Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic landbridge. *American Naturalist* 168: 730–741.
- Romano, P.S.R., and S.A.K. Azevedo. 2006. Are extant podocnemidid turtles relicts of a widespread Cretaceous ancestor? *South American Journal of Herpetology* 1 (3): 175–184.
- Raxworthy, C. J. 2003. Introduction to the reptiles. In S. M. Goodman and J. P. Benstead (editors), *The natural history of Madagascar*: 934–949. Chicago: University of Chicago Press.
- Samonds, K.E., et al. 2009. *Eotheroides lambondrano*, new middle Eocene seacow (Mammalia, Sirenia) from the Mahajanga Basin, northwestern Madagascar. *Journal of Vertebrate Paleontology* 29: 1233–1243.
- Storey, M., et al. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science* 267: 852–855.
- Storey, M., J.J. Mahoney, and A.D. Saunders. 1997. Cretaceous basalts in Madagascar and the transition between plume and continental lithosphere mantle sources. *Geophysical Monograph* 100: 95–122.
- Torsvik, T.H., et al. 2000. Late Cretaceous India-Madagascar fit and timing of break-up related magmatism. *Terra Nova* 12: 220–224.
- Vargas-Ramírez, M., O.V. Castaño-Mora, and U. Fritz. 2008. Molecular phylogeny and divergence times of ancient South American and Malagasy river turtles (Testudines: Pleurodira: Podocnemididae). *Organisms, Diversity, and Evolution* 8: 388–398.

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